X. *Minute structure of the Papillæ and Nerves of the Tongue of the Frog and Toad.*

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THE attention of physiologists was first directed by me to the peculiar advantages possessed by the tongue of the living frog and other similar animals for microscopic investigation, in the year 1839. The extreme elasticity and transparency of this organ induced me to submit it to the microscope, principally with a view of examining the muscles during contraction. I communicated these experiments to M. Donne, who has mentioned my claim of priority in his Cours de Microscopie, p. 108, and they were first made public at the Société Philomatique, Aug. 17, 1839*. It will be unnecessary in a communication addressed to the Royal Society, to occupy the time of that learned body by recapitulating what is already known respecting the organ of taste. I shall therefore proceed at once to describe the results of my further researches on this organ, by which I have been enabled to determine the peculiar structure of the papillæ, and the ultimate termination of the nerves within them. In conclusion, I will point out the deductions which necessarily ensue with regard to the distinct nature of the functions of these organs in the act of taste.

Tongue of the Frog.

In this we find the same component parts as in the tongue of man. The principal points of difference are its smaller size, and the manner in which it is placed in the mouth. In other respects it presents the greatest analogy with that of the human subject. Its frame-work is composed of two muscles, the hyoglossus and the genioglossus. The hyoglossus arises from the inferior border of the body of hyoid bone and ascends to its superior border, the fibres diverging; afterwards it reflects backwards in the throat, the fibres forming a fan-like expansion. The genioglossus is a small, thick, triangular muscle, inserted by its base to the centre of the lower maxillary. The summit terminates near the inner third of the tongue in a tendinous extremity. These two muscles unite at an acute angle, and when at rest hang down the throat. The form of the tongue differs from that of other animals. The anterior extremity is broad, with a notch which divides it into two extremities or tubercles. The precise form of the extremity is best seen when compressed between two slips of glass. In a state of rest the extremity of the tongue hangs down the throat, where it serves as a valve to close the posterior nares in the act of swallowing the air for

* Minutes of which are to be seen in the Journal de l'Institut, p. 316, year 1839.

respiration. It likewise acts as an agent for seizing prey by being rapidly thrown out of the mouth, and enveloping the object to be laid hold of. In this act it is protruded from the mouth by turning round the lower jaw bone as a centre of rotation, the upper surface then becoming lowermost. The lingual arteries and veins are derived from the same trunks as in man, ascend the throat parallel to each other, and enter the tongue between the hyoglossus and the genioglossus. The nerves consist of two pairs, one direct from the brain, the other from the spinal marrow.

Mode of preparing the Frog's Tongue for examination.

In former experiments I confined the animal in a narrow bandage, which I rolled round it from the feet to the neck. In this state all movement of the limbs was completely prevented, while it was still able to carry on respiration. A piece of sheet cork, about the breadth and length of the animal, was then provided, and an opening made near one end of about the size of a shilling. After being secured to this cork, the tongue was turned out of the mouth and stretched over the opening by means of pins. But notwithstanding every care that could be taken it frequently happened that the experiment would be interrupted by the movement of the tongue, and its being torn from the pins. I am now able, by submitting the animal to the action of ether, to avoid these objections. For this purpose I find it most convenient to place the frog in a large wide-mouthed bottle, closed with a ground stopper, and containing ether. To prevent the contact of the ether with the animal's body, where it would produce inflammation, I keep the ether apart in a small phial, which is introduced into the bottle, so that in all the animal's movements it never is affected by the liquid. Placed in this kind of closed chamber, the frog becomes quickly narcotized by the ethereal atmosphere. The cessation of all motion shows the period when insensibility has taken place, and it may be withdrawn and the tongue expanded around the opening as before described. Usually the animals are completely insensible after about five minutes' exposure, and remain in that condition for upwards of half an hour. The insensibility may be prolonged to several hours by leaving them longer in the bottle. An exposure of half an hour generally renders them insensible for two hours. In this way we have the great advantage of avoiding all pain to the animal, independently of rendering the experiment more easy. I find the action of ether perfectly harmless to life, not having observed a single death in consequence of its action, even where it had been prolonged for several hours. A curious anomaly exists with regard to the full-grown female frogs; for I find in my experiments this winter that they are brought under its influence with much greater difficulty than the males and smaller animals, so much so, that after two hours' exposure they are less influenced than one of the latter after five minutes. The advantages of ether are so great that I have abandoned my former method, to which I shall only recur when I have to describe the difference in microscopic appearances in animals that have been etherized from those which have not.

Instead of sulphuric ether we may employ chloroform, muriatic ether, nitric ether, camphor, sulphuret of carbon, naphtha, alcohol, and various other volatile bodies. In some cases it will be found more advantageous to examine only a small portion of the tongue, which may be done by removing a small piece of the membrane with scissors, and interposing it between two slips of glass; this applies more particularly to those animals whose tongues are opake and not elastic.

Burdach has mentioned another method of examining the dead tongue by dipping it into a dilute solution of caustic potash, and then interposing it between the plates of the compressorium. As an auxiliary means, I may mention that by the application of a dilute solution of potash (about twenty parts water to one of liquor potassæ) we may also render the living tongue much more transparent. Another means of preparation is to keep the animal for several days after death, when the maceration of the organ in its own moisture, and the partial state of putrefaction, cause the detachment of the epithelial scales and the uncovering of the subjacent parts. Each of these means will be found to have, in certain cases, its peculiar advantage, and we cannot vary and multiply them too much, as in each case we view nature under a different aspect. As I have described on a former occasion* the principal phenomena connected with circulation in this organ, I will examine now those parts of the tongue which have reference to its sensorial functions of taste and of touch. The nerves which possess these powers are distributed and supported by the tegumentary membranes of the two sides of the tongue, our attention will therefore be directed to the various tissues of which these two membranes consist.

Vibratile Cilia and Rugæ.—The first parts which engage our attention, exclusively of the mucus on the surface, are the vibratile cilia of the tongue. The most active ciliary movement exists at the borders of the tongue. When a minute portion of the membrane is removed, anywhere near the edges and anterior extremity, we generally observe a most active movement at the borders of the fragment, and over its surface we find numerous channels running obliquely outwards and forwards, evidently corresponding to those rugæ we meet with on the human tongue in a similar situation. The ciliary filaments seen down these furrows meet at an obtuse angle, and exhibit a constant undulating movement transmitted downwards from one extremity to the other. Any small body coming into this channel is generally propelled quickly in one direction. Occasionally a succession of blood-particles are seen running down this channel which might easily be mistaken for blood circulating within a capillary. The appearance of the blood-particles viewed with a power of 400 diameters while beaten about by the ciliary filaments is sometimes very curious. The form of the vesicle is seen to vary in the most singular manner, sometimes dilated, sometimes compressed longitudinally or transversely, like a bladder partly filled with water when beaten about with rods. When the fragment has been freshly divided, a general tremor is observed at first, which arises from the irritation of the

* Phil. Mag. vol. xxix.

divided muscular fibres, and which ceases after a short time. The ciliary action, on the contrary, lasts a considerable time, and I have detected it two days after death in some instances. Even in a small detached fragment placed under the microscope I have known it to last for several hours, and it would probably continue still longer if kept moistened with saliva. After remaining about half an hour under examination the border of the tongue is seen to undergo an alteration. The particles of epithelium become uneven and gradually disaggregated. These entirely separate at some spots, and consequently numerous small, uneven cavities are formed along the borders. The surface of the fungiform papillæ is covered with cilia in active motion, while the conical papillæ by the side of them are entirely devoid of them.

The Conical Papillæ over the expanded tongue are found of various forms, conical or cylindrical; sometimes simple, sometimes compound, like so many conical projections seated on one body. We generally succeed in detecting an opening at the summit of each of them. The opening is either sharp at the edges or anal-like with circular lips. From above we see the commencement of a cavity lined with epithelium, which I have been able to see terminate in an infundibular canal extending towards the base of the papilla. These papillæ generally contain no vascular capillaries within them. When they do exist, they never ascend to the summit of the body, but form a bend or loop at about the half or lower third of the height of the cone.

Fungiform Papillæ.—These are easily distinguished from any other bodies on the surface of the tongue, by the existence within them of a coil of capillary vessels generally containing blood in a state of active circulation. They are always larger and redder than the conical papillæ; sometimes they present at the summit a red point of apparently extravasated blood, but which, when examined under a high power, is found to be merely an engorged vessel. A similar appearance on a larger scale is often seen on the fungiform papillæ in man. The fungiform papillæ consist of a circular zone of epithelian cells containing a central area filled with coils of capillary vessels, and with nerve-tubules ascending and terminating abruptly amongst them. When examined on an expanded tongue, we can form no accurate idea of the real elevation of these bodies, as they appear like discs adhering to the membrane subjacent, the stem not being visible; but if we remove a small fragment of the membrane and interpose it between glass, we find them standing out in relief at the borders, and of the same form as in other animals, viz. that of a flask or gourd. Some have a long pedicel, which becomes gradually narrower to its point of insertion to the membrane, where its thickness scarcely equals a fourth or fifth of that of the body. Others are with scarcely anything deserving the name of pedicel; and again some are compound, consisting of either of the above varieties, with the addition of one or two small conical papillæ joined to the external zone.

These varieties arise rather from their position on the tongue, than from any structural distinction. The degree of contraction of the pedicel and its height are connected with the height and size of the conical papillæ around them. Where these are long

and thickly studded, as at the dorsum and base of the tongue, the fungiform are likewise long and generally contracted. At the borders and at the tubercles, where the papillæ conicæ are short, the fungiform are thick, short, and surrounded by a thick protecting membrane of the same nature as in the papillæ conicæ, which in the lengthened fungiform papillæ is much less solid.

By the application of a minute quantity of solution of potash over a fungiform papilla, we sometimes observe a curious appearance. The external zone becomes separated from the central area by a deep fissure, and forms a kind of cup containing the blood-vessel, which appears like a spiral tube, and within this is seen the bundle of nerves. The circulation continues for some time in the papillary vessels even in this denuded state, then becomes languid, and finally ceases when coagulation of the blood takes place, unless the vessels burst at some point and extravasation of blood ensues, which is frequently the case, preventing any further observation.

The vessels of these papillæ are generally derived from arteries and veins, situated near the inferior surface of the tongue, from whence they ascend in a vertical direction until they reach the pedicel of the papilla. At this point the arterial and venous canals appear to be already reduced to the size of the ordinary capillary tubes, and they do not appear to undergo much, if any, further decrease of size in the capillary tuft at the summit. We might at first imagine that these coils are the continuation of one single tube, but such is not the case. They frequently communicate with each other, for when circulation is arrested or impeded in one loop, it often continues in the adjacent ones. They contain no valves such as are found at other parts of the tongue, for after any violent movement of the tongue the circulation often changes its direction, and what was at first an arterial capillary is afterwards found to convey the blood towards the heart like a vein.

Besides blood-vessels and nerves, we invariably discover in the interior of the fungiform papillæ numerous striated muscular fibres. They are derived from the superficial muscular layer, which exists beneath the basement membrane of the dorsum of the tongue, and appear to be one of the essential elements of the mucous tegument of that region. They run parallel with the vessels and nerves, to which they are external, and form a complete investment. After attaining nearly to the summit of the papilla, they curve inwards, and afterwards disappear in the surrounding tissues, apparently by losing their striæ and sarcolemma, which are their distinctive characters. This mode of termination of the fibres is deserving of attention, and is, I believe, the only instance in which the gradual transformation of the muscular element into any other tissue than the fibrous variety composing tendons has been discovered. I have before mentioned the ciliary motion on the surface of these papillæ, and its absence over the other papillæ which are destitute of muscular fibres. We are therefore led to the conclusion that ciliary and muscular power are more closely connected than is commonly imagined. The action of these fibres is to shorten the papilla, probably at the same time they may compress the vessels, regu-

lating to some extent the current of blood, and produce the turgescence of these papillæ which has been observed in the higher animals. The action of the cilia is very evident while under experiment. It conduces to clear away foreign bodies from the surface; to equalize the distribution of the sapid substance over them, and consequently over the nervous extremities; and to promote the removal of the epithelial scales which are constantly being shed.

Nerves of the Papillæ conicæ.—The epithelial scales veil these in general so completely that it is difficult to detect them. The application of the alkali which dissolves the scales, also disorganizes the nerves beneath. The plan which I find the most successful, is to macerate the part for an hour or two in saliva or water, when the increased transparency of the membrane renders the nerves more distinct. They are generally single, rarely two or three running together. Their course is irregular, wavy, with frequent simple loops, which enables them to present a much greater surface. In the tubule we frequently observe small granulations, but no white substance of SCHWANN is detected when perfectly fresh, although it frequently appears after the object has been kept for some time under examination. As a general rule in the conical papillæ, the nerve-tube runs close to the aperture of the papilla around which it forms loops, after which it runs away in a wavy direction. Often at each angle of the aperture is a nerve-loop of this kind formed by separate tubes, besides others which are seen running in a meandering course, and crossing the former in various directions. The space enclosed by these nervous loops is much darker than elsewhere, as if it contained some dark granular matter. The tubes never appear to terminate abruptly in free extremities. They are derived from trunks which give off at nearly regular intervals two or three tubules closely joined together, which afterwards subdivide in a manner more and more irregular, till they reach the state of single nerve-tubules.

It is evident that these are the nerves which convey the sensations of touch to the brain. The situation which they occupy at the base of the conical papillæ underneath the epithelian scales, can leave no doubt in this respect. It is true, that as at the base of the conical papillæ, and immediately beneath the epithelian scales, we find striated muscular fibres running in various directions, and some ascending into the interior of the body of the fungiform papillæ, it might be surmised whether these nerves are not destined to excite the contractile powers of these fibres. But their development, so utterly disproportioned to the office of stimulating a few muscular fibres, their mode of distribution in loops and convolutions, and their separation into single or double tubules, prevent our regarding them as muscular nerves. A curious point in reference to the nerves of touch, especially in the skin, are the fruitless attempts that have been made by numerous observers, to detect their ultimate terminations in the interior of the papillæ. On account of the impossibility of seeing the nerve-tubules within the papillæ, it has been imagined by some that they lose their external covering, and that they experience a gradual fusion with the

papillary structure which must effectually prevent our seeing them in these tissues. In my researches on the frog's tongue, I have never observed any alteration in the appearance of the tubules in support of this hypothesis, which I am therefore led to reject. In searching for the extremities of these nerves, which for brevity I will term the tactile nerves, in opposition to the others which are either gustatory or muscular, I experience considerable difficulty in detecting them until one or two simple tubes are seen, which being followed for some distance, serve as a clue to numerous other convolutions around them. By this means a spot which a moment before appeared covered with epithelium and destitute of nerves, is seen to be covered with abundant nerve-tubes distributed in the way I have mentioned. If such is the case with regard to the nearly transparent epithelium and papillæ of the frog, how much more so must it be the case in the papillæ of the skin, where observers have hitherto sought them, and where they are obliged to employ chemical agents to increase the transparency of this membrane!

To attain a view of their terminations, we are obliged to flatten the papillæ by compression. In this state we cannot determine to what height the nerves ascend within them. I have repeatedly in vain attempted to trace the nerve in the conical papillæ, seen in section at the borders of a fragment, while at the same time in an adjacent fungiform papilla I have obtained a perfect sight of the gustatory nerves. The farthest points to which I have followed them in these circumstances has been to their base, where the capillaries and the muscular fibres form a kind of basement structure. Here the nerves are found agglomerated together in knots, wherein the continuity of the tubules could not be traced. These knots were probably of a ganglionic nature. Over the vessels nerve-tubules of about one-third of the size of ordinary nerve-tubes were sometimes seen.

Nerves of the Fungiform Papillæ.—The papillary nerve may be seen at some distance before it reaches the pedicel, to form numerous waving incurvations, which appear to increase as it approaches it. Near the pedicel we usually perceive a kind of knot which contains numerous loops of the nerve. Before it reaches this knot, it is found to be composed of separate nerve-tubules, generally not more than five or six in number. If not sufficiently distinct, it may be rendered more so by a drop of alkali which dissolves the epithelium. In following the nerve to the pedicel, we perceive that it becomes darker, its fibres more confused, and occasionally with vesicular granules interposed between the tubules. When the expanded tongue is seen with a low power, the nervous knot at the pedicel is almost invariably detected by its dark-grey aspect and numerous loops. After forming this intricate arrangement, the nerve-tubules ascend into the interior of the papillæ, and expanding, become less dark. By the use of the compressorium and the alkali we are enabled to see their termination with ease. After nearly attaining the summit of the papillæ, we find some of the tubules to separate from the main body at an acute angle, proceeding until they reach some of the capillary vessels, where each tubule terminates abruptly, most

frequently with an irregular pointed extremity. The rest of the tubes still continue in close contact, and when they have attained the membrane of the area, end abruptly in an irregular manner, some in a point, some club-shaped, some in a spiral form, others like small funnels, but most often with a kind of concentric mouth.

In some papillæ the nerve-tubes keep close together until their termination, which takes place immediately at the surface of the area at its central point. Their open mouths are closely joined, and almost interlaced with one another. In others the terminations of the nerve are still more evident, for the tubes are seen expanding and crossing over each other so as to supply as equally as possible each of the areas enclosed by the capillary loops.

Nerves of the inferior surface of the tongue.—This surface presents neither conical nor fungiform papillæ. Its epithelium consists of flat nucleated scales, extremely thin. In a portion of this surface removed from the organ and interposed between glass, we may detect abundant convolutions of the nerves, similar in every respect to those found under the conical papillæ; they are very tortuous, form frequent loops, and are reduced to the state of nearly single tubes.

Mucous follicles.—These are seen over various parts of the upper surface interspersed among the papillæ. Their appearance at the surface is that of an anal opening generally closed during life, forming a slightly prominent tumid ring. After death, or when the membrane is much distended, the eye penetrates into their interior, where an active ciliary motion exists. When the surrounding membrane is denuded of its scales, we perceive around the opening two striated muscular fibres, forming a curve on each side, and performing the office of a sphincter. The follicle forms a bottle-shaped cavity, exactly like the small follicles over the skin of the frog, particularly near the anus. It is supplied by a capillary which runs close by it, without encircling or spreading over it. The follicular nerve consists of one or two tubules, and makes a single or double coil when it reaches the follicle.

In recapitulating these observations, we find in the frog an organ of taste similar in its general structure to that in man. At the upper surface are bodies corresponding to the conical and fungiform papillæ. At the inferior surface the membrane is smooth and without anything of the kind. We may therefore conclude that the upper surface has the faculty of taste and of touch, and that the under surface is merely tactile as in our own species. The fungiform papillæ consist of a membranous vesicle or utricule, containing coils of capillaries, numerous nerves, and muscular fibres, and probably lymphatics. Where do the nervous elements which these bodies contain extend themselves? We invariably find that they terminate at a part of the utricule where the membrane is so transparent that we may almost doubt whether they are surrounded at all by a membrane. This is the area which I term the *gustatory* or *neuro-vascular*, where the action of the nervous radicels is performed, which being conveyed to the brain excites an impression of taste. Another element observed in this area is the existence of numerous and intricate coils of capillary vessels

which surround the nervous extremities in all directions. We find also a zone or belt which encircles the gustatory area, and serves principally to protect and support it. Numerous muscular fibres are directed towards this zone, which will account for the partial erectility of the fungiform papillæ on certain occasions.

The gustatory area is placed sometimes at the extremity, at others at the sides of the papillæ. Whether this difference in situation be connected or not with any difference of sensation, it is impossible to determine; but in each case the gustatory area is placed conveniently near to any liquid spread over the tongue. It is further observed that the height of these papillæ varies with that of the surrounding papillæ conicæ. We are well-aware that it is only when in solution bodies can be tasted. The trituration of substances in the mouth has the effect of producing this wherever it is possible. When once in this condition, we cannot but admire the beautiful and simple structural arrangement by which taste is effected. The membrane of the gustatory area is so exceedingly thin that the transudation of any liquid in contact with it must be proportionately rapid. Accordingly, the open extremities of the nerves may be considered as immersed into the solution which it has to analyse, whether to reject, or to allow to pass on to the stomach. The mysterious action by which the material world comes in contact with mind, is being effected under our closest scrutiny. If we are ever to penetrate further into the arcana of life, may we not expect to do so by observing these phenomena while the vital powers are intact? While the nerve is being stimulated, the current within the capillary coil is continuing its course, and it requires but a slight acquaintance with the laws of imbibition to recognize that in this case the sapid solution must be rapidly eliminated, and that the nerve will consequently be free from its presence, and fresh to receive a new impression.

Tongue of the Toad.

Unlike what might have been expected from the habits of this animal, its organ of taste is less developed than that of the frog. The tongue is of a similar structure and form, and is covered with papillæ more minute and simple. The fungiform papillæ are less numerous. In the full-grown animal they present at their summit a circular capillary enclosing a fasciculus of nerve-tubes closely joined together. They also contain muscular fibres, and are provided with cilia.

The conical papillæ are less distinct, and are composed rather of folds or rugæ of the membrane than of separate bodies. On comparing a frog and toad of the same size, we find in the latter the papillæ much less developed. Taking, for example, a toad weighing five drachms, we find the epithelian scales over the dorsum very indistinct, and the surface finely granular. The fungiform papillæ are the $\frac{1}{380}$th of an inch in thickness, without any pedicel. The blood-vessels form two or three loops at the summit of the papilla. The nerve-tubules are much less numerous than those of the frog, less distinct and extremely varicose. The summit of the papilla consists

of a granular mass of a convex form, which, when viewed at the edges, appears surrounded by a fringe of epithelial cells, which is detached after a short maceration. The conical papillæ rarely exceed the $\frac{1}{1200}$th of an inch in height. Maceration causes them to swell considerably, so as to attain more than double their original size. The greatest increase is at their summit or free extremity, and the papilla then assumes a flask-like form. Some of the epithelial cells likewise attain an extraordinary increase of size by maceration.

Description of the Plate.

PLATE XII.

A portion of the frog's tongue removed from the border near one of the tubercles, as viewed with a magnifying power of 350 diameters, under a slight compression.

A. Fungiform papilla, projecting along the margin.

B. B. Conical papillæ, projecting along the margin.

C. Border of the tongue with vibratile cilia, seen in constant movement over the fungiform papillæ. The depression in the border is the commencement of a channel formed by the rugæ so numerous near the edges.

D. Small mucous follicle.

E. Apertures of the conical papillæ.

F. A capillary vessel containing blood-discs and corpuscles, ascending halfway up the papilla conica.

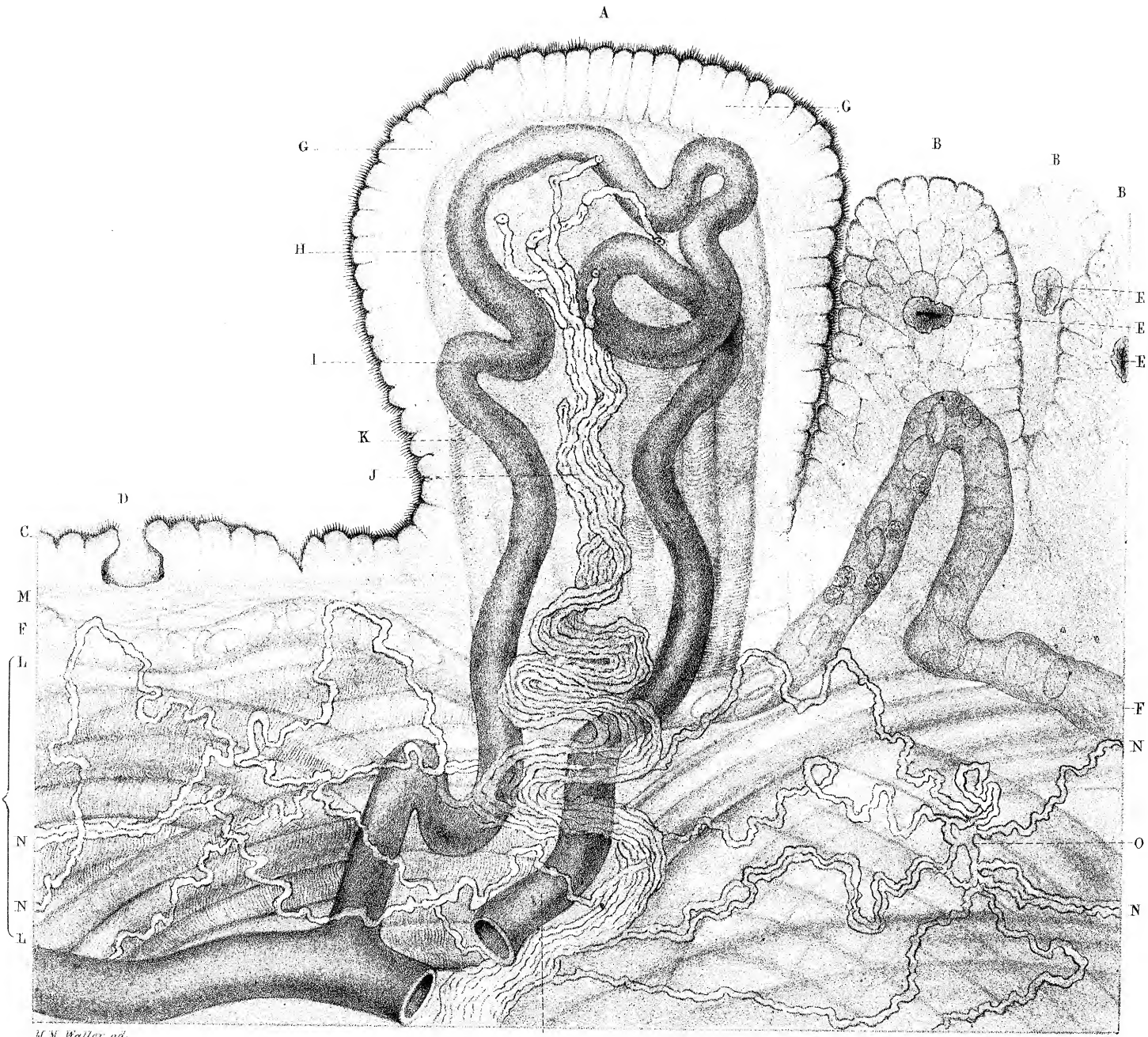
G. External zone of fungiform papilla, formed of epithelian cells which are much more indistinct and laminated over the neuro-vascular area.

H. Neuro-vascular area containing the capillary, the gustatory nerve, and striated muscular fibre.

I. The capillary ascending from the lower surface of the tongue towards the fungiform papilla, wherein it forms coils, making its exit in the same direction in which it entered. The vessel is represented in a state of engorgement, the globules compressed and indistinct.

J. The gustatory nerve, likewise derived from a branch near the inferior surface, entering the papilla between the capillary. Near its entrance it makes numerous wavy bends of a spiral form. The tubules become more distinct and diffused towards their extremities, where they appear to be composed of separate joints from the coagulation of the medulla of the tubule. Their extremities in this example appeared all of them to be slightly dilated, and with a dark point at their termination, giving them the appearance of ending in open mouths.

K. Striped muscular fibres ascending vertically into the papilla among the vessels and nerves, becoming indistinct near the summit.



M.M. Waller, ad. naturam del.

J. Basire, lith.

Scale $\frac{mm}{} = 0.05 = \frac{inch}{} 0.1968.$

L. Striated muscular fibres, forming hoops or circles beneath the mucous membrane; they are left plain to the right of the drawing to avoid complicating the figure.

M. Fibrous tissue of an elastic nature beneath the epithelium.

N. Tactile nerves forming a network over the muscular fibre. They merely attain the base of the conical papillæ.

O. An agglomeration of nerve-tubules. In this instance they appeared to be in part derived from the gustatory nerve before its ascent into the papilla.